第 37 卷第 6 期
2017 年 3 月

生 态 学 报
ACTA ECOLOGICA SINICA

Vol.37,No.6
Mar.,2017

DOI: 10.5846/stxb201511112288

董彬,韩睿明,王国祥.沉水植物茎叶微界面特性研究进展.生态学报,2017,37(6):1769-1776.

Dong B, Han R M, Wang G X.Research advances in and perspectives on characteristics of the micro-boundary layer around leaves and stems of submerged macrophytes.Acta Ecologica Sinica,2017,37(6):1769-1776.

沉水植物茎叶微界面特性研究进展

董 彬[1,*],韩睿明[2,3],王国祥[2,3]

1 临沂大学资源环境学院, 临沂 276000

2 南京师范大学环境学院, 南京 210023

3 江苏省地理信息资源开发与利用协同创新中心, 南京 210023

摘要:沉水植物茎叶-水界面是浅水湖泊的重要界面之一,对湖泊生物地球化学循环和水环境质量具有重要影响。富营养化水体中,大量的附着物常富集在沉水植物茎叶表面,形成了特殊的生物-水微界面。对该微界面特性进行深入研究,有助于揭示沉水植物在微环境层面对富营养化水体中物质循环的调控过程和机制。沉水植物茎叶微界面具有促进水体养分转化、改变环境因子及可溶性物质的空间分布,增加物质运输的阻力和距离、降低植物光合作用、调控重金属等生态功能;微界面结构及环境因子受水体营养盐浓度、沉水植物种类及生长阶段等因素的影响。对微界面结构功能的主要研究方法进行了分析总结,并对沉水植物茎叶微界面的研究前沿进行了展望。

关键词:沉水植物;微界面;功能;富营养化

Research advances in and perspectives on characteristics of the micro-boundary layer around leaves and stems of submerged macrophytes

DONG Bin[1,*], HAN Ruiming[2,3], WANG Guoxiang[2,3]

1 *College of Resource and Environment, Linyi University, Linyi* 276000, *China*

2 *School of Environment, Nanjing Normal University, Nanjing* 210023, *China*

3 *Jiangsu Center for Collaborative Innovation in Geographical Information Resource Development and Application, Nanjing* 210023, *China*

Abstract: Submerged macrophytes constitute an important component of shallow aquatic ecosystems. They provide most of the accessible surface area, constant survival substrates, and available nutrients for periphyton, which remains attached to the stem and leaf surfaces of submerged macrophytes and forms a special bio-water boundary layer. As one of the most important interfaces in shallow lakes, the submerged macrophyte-water boundary layer plays roles in macrophyte growth, biogeochemical cycling, water environment maintenance, and ecological regulation. The present study summarizes the research advancements regarding characteristics of the micro-boundary layer (MBL) around leaves and stems of submerged macrophytes. The ecological functions, biotic and environmental factors, and research methods are identified and reviewed. Perspectives for the focus of future research on MBL around submerged macrophytes are raised.The MBL around submerged macrophytes has important ecological functions. The dense periphyton in MBL exerts negative effects on photosynthesis in submerged macrophytes, creates a barrier hindering the transport of dissolved substances, such as O_2, and leads to the degradation and even disappearance of submerged macrophytes in eutrophic waters. The plant stress derived from pollutants may be alleviated because of the periphytic barrier in the MBL. The epiphytic bacteria in the MBL can be of considerable

基金项目:国家自然科学基金资助项目(41173078,41403064);江苏省自然科学基金青年基金资助项目(BK20140922);江苏省教育厅高校自然科学研究面上项目(14KJB610007)

收稿日期:2015-11-11; **网络出版日期**:2016-08-02

* 通讯作者 Corresponding author.E-mail: dongbin@lyu.edu.cn

importance for nutrient transformation and cycling in eutrophic ecosystems. Periphyton is an assemblage of algae, bacteria, fungi, protozoan, inorganic matter, and organic detritus that remains attached to submerged macrophyte surfaces where significant spatio-temporal variations exist in the MBL. The heterogeneity of micro-environmental parameters is the key factor shaping the MBL around submerged macrophytes, given the complex constituents, changing spatial structure, and fluctuation of oxidation-reduction status within this microcosm. At the spatial heterogeneity, in the vertical direction of stem and leaf surfaces, O_2 concentration and pH in the MBL increase markedly with decreasing distance to the surface of leaves and stems and peak at the surface. The trend of the oxidation-reduction potential (ORP) is reverse. Plant species and growing stages are biotic factors that affect the MBL, and nutrients load, light intensity, flow velocity, and habitat are the major environmental factors. The growth stages of macrophytes create large fluctuations and dynamics in O_2, pH, ORP, and soluble substrates at the surface of stems and leaves by changing the thickness of the diffusive boundary layer around the macrophyte. O_2 concentration and pH in the MBL around the leaves and stems of submerged macrophytes increase when macrophytes begin the rapid growing stage, which is accompanied by gradually increasing spatial differentiation. O_2 concentration and pH in the MBL around the leaves and stems reach peaks at the stable growth stage, and increase slightly or decline when the periphyton layer begins the declining stage. However, the ORP shows the opposite trend to that of O_2, and pH. MBL is mainly affected synergistically by plant physiological and periphyton characteristics during the life cycle of macrophytes. Environmental factors affect the MBL via periphyton composition, periphyton mass, and macrophytes growth. Scanning electron microscopy, high spatial resolution of microsensors, microchemical analysis, molecular biology techniques, and isotope tracer techniques are applicable approaches for the study of the characteristics of MBL; however, they have not yet been comprehensively utilization. To further investigate the leaf and stem MBL, we must focus on establishing standard methods and models of the MBL structure and functions to verify the modulation processes and mechanism of the MBL on the biogeochemical cycling in eutrophicated waters. Long-term ecological research under controlled conditions is required.

Key Words: submerged macrophytes; micro-boundary layer; functions; eutrophication

富营养化水体中,大量的藻类、微生物、颗粒物、碎屑等附着在沉水植物茎叶表面,形成了特殊的生物-水微界面[1-3]。沉水植物茎叶微界面是浅水湖泊的重要界面之一,对湖泊生物地球化学循环和水环境质量具有重要影响[4]。由于茎叶微界面内附着物复杂的物质组成,光合作用和异养过程都有可能在微界面内发生,可能会出现因这些生物通过代谢消耗或生产而造成的陡化学梯度分布。因此,微界面内环境因子及溶解性物质的分布可能与在上覆水中的分布存在很大差异[1,5-6]。微界面附着物及其内氧化还原异质微环境对植物生长发育和生态系统的养分迁移转化可能具有重要的影响[7-9]。沉水植物茎叶微界面作为一种特殊的微界面,关于其特性的知识可以丰富人们对茎叶微界面结构和生态功能的认识,加深对沉水植物对水环境生态调控功能的理解,促进沉水植物茎叶微界面对富营养化水体物质迁移转化的调控过程和机制的研究。本文在总结分析当前国内外文献的基础上,对沉水植物茎叶微界面生态功能、影响因素和研究方法进行了综述和分析,并对沉水植物茎叶微界面的研究前沿进行了展望。

1 沉水植物茎叶微界面生态功能

1.1 调控水体中营养物质的迁移转化

环境微界面是在相对微观的环境中,对物质交换、转移、转化、反应等具有影响的非均相介质间的微观界面[10]。沉水植物茎叶微界面由于植物的代谢作用和附着层内好氧有机质的分解作用而存在相互分异的氧化-还原微环境,是有机物降解、物质循环及生命活动最强烈的场所,为物质的交换、降解、转化和沉积等提供了环境条件[11-13]。沉水植物茎叶微界面附着物还为营养物质的迁移转化提供了物质和能源条件[14]。沉水植

物由于具有比较大的比表面积,为附着物提供了巨大的附着表面。微界面附着物可大量富集水体中的氮磷和有机质,植物-附着物亦可释放大量的可溶性有机碳(DOC),平均释放速率可达 4.57 mgC m^{-2} h^{-1}[15],为养分的转化提供物质基础。附着藻类可通过吸附颗粒物、自身生长吸收营养盐、光合作用和代谢活动改变水体中的溶解氧(DO)、pH 值等理化条件促进水体中营养物质的迁移转化[16-17]。沉水植物茎叶表面还为附着细菌提供了巨大的生态位[18-19],克隆测序的研究表明沉水植物附着细菌的 OTU 在几十到上百的范围内[20]。在群落结构上,*Betaproteobacteria*、*Bacteroidetes*、*Alphaproteobacteria*、*Actinobacteria*、*Planctomycetes*、*Cyanobacteria* 等门类的细菌较为常见[21],其中包括大量的参与物质循环过程的功能菌,大量碳、氮、磷等相关功能菌促进了营养物质的转化[22]。目前的研究仅初步揭示了附着细菌在元素循环过程中的功能及作用,但鲜有文献涉及其机理方面的信息。

沉水植物茎叶微界面附着物主要是通过 P 吸收和促进磷的沉淀、过滤水体中颗粒态的磷,通过光合作用升高水体的 pH,加速 Ca-P 和碳酸盐-磷酸盐复合体的沉淀[16],促进磷的迁移转化。同时,沉水植物茎叶微界面是水中氨化、反硝化及厌氧氨氧化等脱氮行为机制的重要载体。沉水植物微界面附着物能通过水体理化条件、流速、自身吸收和硝化反硝化等途径对水体氮循环产生影响[7,23-24]。Eriksson 等经多年对富营养化水体中篦齿眼子菜(*Potamogeton pectinatus*)附着生物反硝化作用进行研究,发现附着生物反硝化作用比较重要,可与沉积物的相当[7, 25]。Toet 等发现污水处理厂出水的湿地中伊乐藻(*Elodea nuttallii*)附着生物的反硝化作用速率(14.8—33.1 mg N m^{-2} d^{-1})显著高于(0.5—25.5 mg N m^{-2} d^{-1})和水体的(0.4—3.9 mg N m^{-2} d^{-1})[8]。现有研究在一定程度上显示了微界面对氮磷的迁移转化具有明显促进作用,可能进而将影响水生态系统的功能。与对海洋、湖泊沉积物-水界面物质迁移转化的深入研究相比[26-27],对淡水植物-水界面的物质迁移转化的研究相对较少[7, 28],难以揭示微界面物质迁移转化的过程和机制。

1.2　改变环境因子及可溶性物质的空间分布,增加物质运输的阻力和距离

一般来说,微界面厚度越大,环境因子及可溶性物质的分布梯度越陡,物质扩散的阻力和距离越大[1,3,6]。微界面的厚度一般通过氧气(O_2)产生的波动结合镜下观测表征,厚度从几十微米至几个毫米不等[1,3,6]。微界面厚度主要受附着层厚度、水体流速[29]、养分浓度、光照、温度等因素的影响。运用微电极技术测定水生植物菹草(*Potamogeton crispus*)[3, 6]马来眼子菜(*Potamogeton malaianus*)[1]、大叶藻(*Zostera marina*)和宣藻(*Scytosiphon lomentaria*)[5]叶微界面 O_2和 pH,发现空间上(2 mm 范围内),在垂直叶片表面方向由外向内,越接近植物叶表面 O_2浓度和 pH 越高,空间分布梯度越明显,而氧化还原电位(ORP)则越接近叶表面越低[1]。初步的研究表明:在附着层较厚的沉水植物微界面内,环境因子 O_2浓度和 pH 分布梯度较陡,空间差异较大,去除附着物这一屏障后,波动幅度明显减小[1, 3, 6],氧化还原电位亦存在类似的变化[1]。目前对其他溶解物质空间分布的研究尚比较少见。

沉水植物叶表附着物的存在可增加微界面厚度,使游离态 O_2、二氧化碳(CO_2)、可溶性无机碳(DIC)、DOC、氮、磷等可溶物质运输和扩散的距离和阻力增加[2, 15, 30]。叶表面游离态 O_2通量可通过菲克第一定律(Fick′s first law)计算,董彬等发现去除附着层之后,马来眼子菜成熟茎叶微界面 O_2通量明显增加了[1],表明微界面附着层阻碍了 O_2从茎叶表面向水体的迁移和扩散。微界面内其他溶解物质的运输过程在沉积物-水界面、根-沉积物界面以及废水生物膜中已得到深入研究[31-33],但由于对沉水植物具有生理代谢活性,给茎叶微界面物质运输研究带来了一定的困难,致使微界面其他可溶性物质分布的研究尚未得到开展。

1.3　降低植物光合作用

沉水植物茎叶微界面附着物可通过遮荫和资源竞争减缓植物光合作用和生长。光通过附着层到达植物叶表面时会发生衰减,附着层厚度越大光衰减越多;光衰减在一定条件下会降低沉水植物的光合作用速率,最终对植物生长产生重要影响[34]。Jones 等发现由于附着生物对水中 CO_2的利用,使沉水植物叶微界面 CO_2浓度降低至 2 μmol/L,无机碳浓度成为沉水植物光合作用的关键限制因子,对沉水植物光合作用产生了不利影响[35]。微界面附着物可使沉水植物叶绿素含量发生改变、叶片枯死量增加和光合作用产量下降[1, 36]。

Laugaste 等认为:在富营养化湖泊藻类暴发过程中,首先发生附着生物的大量增殖,而后才发生浮游藻类暴发,并指出附着生物的大量繁殖可能是藻类暴发和沉水植物消亡的重要诱因[37]。附着生物的大量增殖可能是富营养化水体中沉水植物消亡的一个重要原因,但在附着生物大量增殖是否是沉水植物消亡的最直接原因这一问题上,目前的观点并不一致[38-39]。一部分学者认为,由于浮游藻类大量繁殖所导致的水体透明度降低以及遮光作用所引起的水下光照缺乏是沉水植物消亡的直接原因;但还有人认为是附着生物与水生植物对营养盐和光等生态资源的竞争以及其产生的代谢产物对沉水植物光合作用的抑制,可能是造成沉水植物在富营养化水体中退化的关键[40]。研究证实,附着生物对沉水植物的抑制作用比营养盐更加直接,对沉水植物产生遮荫和资源竞争作用,降低了沉水植物的光合作用,影响了沉水植物的生长发育,加速沉水植物退化甚至消失[6, 9, 41]。

1.4 对重金属的调控作用

与挺水植物和浮叶植物相比,沉水植物对水体中的重金属有较强的吸收作用,主要通过吸附-解吸、沉积-溶解、离子交换、螯合-分解和氧化-还原反应等过程进行[42-43],重金属进入沉水植物体内后,主要以螯合态和毒性较大的可溶态的形式存在。重金属离子在进入植物前首先接触微界面附着物这一高度异质性环境,其中的附着藻类可吸收重金属[44];其中的非生物有机成分可与重金属离子结合,降低重金属离子活度,调节重金属吸收速率;其中的氧化还原微环境可能改变重金属离子理化反应活性,影响重金属吸收速率。因此,理论上沉水植物茎叶微界面附着物在水体重金属离子进入植物茎叶过程中发挥一定的调控作用。虽然对沉水植物吸收重金属的研究已相当深入细致,但沉水植物茎叶微界面对重金属的调控作用的研究尚比较欠缺,但具体的调控过程和机制还有待进一步探究。

2 沉水植物茎叶微界面的影响因素

沉水植物茎叶微界面的影响因素比较多,如植物种类、生长阶段、光照、水体营养状态、流速、生境等均可对微界面结构和功能产生影响。不同种类的植物叶片由于其独特的化学组成、物理结构、叶片分泌或渗出的物质,如糖类、脂蛋白、有机酸、酚类等,它们作为微生物和藻类细菌生长的营养物质、干扰物质或者信号转导物质,都会对微界面附着物的结构、数量和多样性造成影响[19]。随着植物进入生长期,附着物持续增加,附着层和扩散边界层厚度逐渐增大,植物生理活性逐渐增强,微界面环境因子如 DO、pH 和 ORP 波动幅度和空间差异逐渐增大;进入衰亡期,则出现相反的变化趋势。在生长期,由于附着物比较稀疏,微界面主要受植物的影响。在衰亡期,由于植物生理活性的降低和附着物的持续积累增厚,微界面主要受附着物的影响[3]。

光照对植物茎叶微界面的影响主要体现在两个空间等级。光照随着水体深度的增加而减弱,也会随着进入附着生物内部的深度而削弱。光照随着深度的增加而减弱主要是受悬浮固体的影响,进而影响植物生长和附着生物的群落组成[45]。附着生物随着深度梯度受光照调节而形成群落结构、外形、密度和功能上的差异。附着生物群落自身也可以强烈地减弱光照,能够极大的改变到达宿主植物的光照质量[46]。水体营养状态可影响微界面厚度和结构。微界面附着物是水生态系统中的重要化学调节器,在其生长过程中能大量吸收水体和宿主中的养分。随着营养盐负荷的增加,沉水植物茎叶微界面附着物增加[9, 47]。在超富营养化水体中,透明度较低,但附着生物比浮游藻类更能适应低光强环境;在较高浓度的氮、磷和光照充足的情况下,附着生物的生物量能达到最大,对氮、磷的吸收和转化率也较高。水体流速对微界面的影响研究主要集中在沉积物-水微界面[48]和生物膜[49]上,对沉水植物-水微界面的研究较少[50-51]。一般来说,随着流速的增大,微界面厚度降低,附着物厚度降低,促进微界面物质迁移转化[48, 51]。

3 研究方法

3.1 对微界面结构的研究

对沉水植物茎叶微界面结构研究方法进行了分析总结(表 1)。光学显微镜只能大体观测到微界面的表

面结构,协助检测微界面附着物的全貌。声学和光学速度计可用来描述附着生物群落附近和内部的水力条件、去向和来自附着生物的边界层运输。后来发展起来的扫描电镜技术大大促进了人们对微界面结构的了解[52-54]。其中环境扫描电子显微镜,沉水植物样品可不经任何前处理,在环境真空条件下直接分析的微界面结构,可更直观地呈现微界面的真实结构,是研究沉水植物茎叶微界面结构的理想工具。

表 1　沉水植物茎叶微界面结构研究方法比较

Table 1　Comparation of research methods for mciro-boundary layer structure around submerged macrophytes leaves and stems

研究方法 Research methods	优点 Advantages	缺点 Disadvantages
光学显微镜 OM	宏观上观测微界面附着物表面,协助检测微界面全貌	不能研究植物-附着物的复杂关系
普通扫描电镜[52-54] SEM	可在较小尺度上研究微界面附着物结构	需对植物样品进行脱水等前处理,易造成附着物脱落,不能反映其真实结构
激光扫描共聚焦显微镜 CLSM[55]	可在精细尺度上研究微界面附着物结构	需做切片,易对微界面附着物造成挤压变形
冷冻扫描电镜 Cryo- SEM	使水在低温状态下呈玻璃态,减少冰晶的产生,可获得微界面的真实形貌	需超低温冷冻、断裂、镀膜制样(喷金/喷碳)等前处理,成本较高
环境扫描电镜 ESEM	无需对样品进行前处理,可在微米尺度上研究完整的微界面真实结构	

3.2　对微界面环境因子和可溶性物质分布的研究

近几十年发展起来的微电极和光纤技术使研究者可在微界面内进行精细的生物地球化学剖面研究[1,56-57],可在较小的时空尺度上测定微界面内理化变量的空间分布,且对样品无明显干扰。目前主要有光纤微电极和电化学微电极两类。微电极目前多用于研究沉积物-水界面[58]、藻垫[59]、生物膜[60]、根际[61]和沉水植物叶片[1,6]等的微环境中 DO、pH、氧化还原电位(ORP)、NO_3^-、NO_2^-、NH_4^+、H_2S、CO_2、NO、N_2O 等的微尺度分布。其中对沉水植物茎、叶微界面的研究还相对较少,这与沉水植物微界面的重要作用极不相符。对沉水植物茎叶微界面微生物的研究主要采用现代分子生物学手段,基于 16S rDNA 的变形梯度凝胶电泳(DGGE)及克隆文库测序和高通量测序技术可用来研究附着细菌的群落结构;采用定量 PCR 技术和基因芯片(Geochip)技术[62]可用来对碳、氮、磷、硫循环等相关功能基因片段进行定量研究。目前对沉积物-微界面和废水生物膜中物质运输的研究多采用微电极方法结合分子生物学手段进行,对沉水植物茎叶微界面来说应用尚存在一定的难度。总之,对微界面的研究方法和技术虽然取得了初步的成果,但仍有待进一步完善和改进。

4　研究展望

近几十年来,淡水沉水植物茎叶微界面的研究得到了快速发展,对沉水植物茎叶微界面附着微生物、藻类、微界面理化指标、硝化作用、反硝化作用过程以及氮循环主要功能细菌已展开研究,并逐渐受到越来越多的关注。但是,由于沉水植物茎叶微界面的研究涉及植物生理生态学、环境化学、生物地球化学和微生物学等多种学科,同时还有赖于先进的分析测试手段和微观观测手段的融合,因此对沉水植物茎叶微界面特性的研究亟需加强。今后的研究重点应集中在如下几方面:

(1)建立沉水植物微界面各指标的测定方法。综合利用扫描电镜技术、高分辨率微电极测定技术、微量化学分析技术、分子生物学技术和同位素示踪技术,对沉水植物茎叶微界面结构组成、环境特征及影响因素等进行深入研究,揭示微界面的时空变化规律,阐明微界面在富营养化水体中的生态功能。

(2)加强沉水植物茎叶微界面养分物质迁移转化主要过程的研究,探明微界面结构组成与养分转化功能的耦合关系,揭示微界面结构组成、微环境变化对养分循环的驱动和调控机制。

(3)在野外调查研究的基础上,开展受控条件下的实验室长期研究,探讨不同影响因素下沉水植物微界面的结构特征及功能变化,进一步建立可溶物质的分布和运输模型,提出沉水植物茎叶微界面理论。

参考文献(References):

[1] Dong B, Han R M, Wang G X, Cao X. O_2, pH, and redox potential microprofiles around *Potamogeton malaianus* measured using microsensors.

PLoS One, 2014, 9(7): e101825.

[2] Sand-Jensen K. Environmental variables and their effect on photosynthesis of aquatic plant communities. Aquatic Botany, 1989, 34(1/3): 5-25.

[3] 董彬, 韩睿明, 王国祥, 毛丽娜, 冀峰, 马杰. 菹草茎叶微界面 O_2时空动态. 生态学报, 2015, 35(24): 8202-8210.

[4] Mei X Y, Zhang X F. Periphyton biomass response to Phosphorus additions in an aquatic ecosystem dominated by submersed plants. Journal of Environmental Protection, 2013, 4(1): 83-90.

[5] Sand-Jensen K, Revsbech N P. Photosynthesis and light adaptation in epiphyte-macrophyte associations measured by oxygen microelectrodes. Limnology and Oceanography, 1987, 32(2): 452-557.

[6] Sand-Jensen K, Revsbech N P, Jørgensen B B. Microprofiles of oxygen in epiphyte communities on submerged macrophytes. Marine Biology, 1985, 89(1): 55-62.

[7] Eriksson P G. Interaction effects of flow velocity and oxygen metabolism on nitrification and denitrification in biofilms on submersed macrophytes. Biogeochemistry, 2001, 55(1): 29-54.

[8] Toet S, Huibers L H F A, Van Logtestijn R S P, Verhoeven J T A. Denitrification in the periphyton associated with plant shoots and in the sediment of a wetland system supplied with sewage treatment plant effluent. Hydrobiologia, 2003, 501(1/3): 29-54.

[9] 董彬, 陆全平, 王国祥, 毛丽娜, 林海, 周锋, 魏宏农. 菹草(*Potamogeton crispus*)附着物对水体氮、磷负荷的响应. 湖泊科学, 2013, 25(3): 359-365.

[10] 曲久辉, 贺泓, 刘会娟. 典型环境微界面及其对污染物环境行为的影响. 环境科学学报, 2009, 29(1): 2-10.

[11] Risgaard-Petersen N, Jensen K. Nitrification and denitrification in the rhizosphere of the aquatic macrophyte *Lobelia dortmanna* L. Limnology and Oceanography, 1997, 42(3): 529-537.

[12] Saralov A I, Galyamina V V, Belyaeva P G, Mol'kov D V. Nitrogen fixation and denitrification in plankton and periphyton of the Kama River Basin watercourses. Inland Water Biology, 2010, 3(2): 112-118.

[13] Coci M, Bodelier P L E, Laanbroek H J. Epiphyton as a niche for ammonia-oxidizing bacteria: detailed comparison with benthic and pelagic compartments in shallow freshwater lakes. Applied and Environmental Microbiology, 2008, 74(7): 1963-1971.

[14] Nielsen L P, Christensen P B, Revsbech N P, Sørensen J. Denitrification and oxygen respiration in biofilms studied with a microsensor for nitrous oxide and oxygen. Microbial Ecology, 1990, 19(1): 63-72.

[15] Demarty M, Prairie Y T. In situ dissolved organic carbon (DOC) release by submerged macrophyte-epiphyte communities in southern Quebec lakes. Canadian Journal of Fisheries and Aquatic Sciences, 2009, 66(9): 1522-1531.

[16] Dodds W K. The role of periphyton in phosphorus retention in shallow freshwater aquatic systems. Journal of Phycology, 2003, 39(5): 840-849.

[17] 秦伯强, 宋玉芝, 高光. 附着生物在浅水富营养化湖泊藻-草型生态系统转化过程中的作用. 中国科学 C 辑 生命科学, 2006, 36(3): 283-288.

[18] Körner S. Nitrifying and denitrifying bacteria in epiphytic communities of submerged macrophytes in a treated sewage channel. Acta Hydrochimica et Hydrobiologica, 1999, 27(1): 27-31.

[19] 何聃, 任丽娟, 邢鹏, 吴庆龙. 沉水植物附着细菌群落结构及其多样性研究进展. 生命科学, 2014, 26(2): 161-168.

[20] He D, Ren L J, Wu Q L. Epiphytic bacterial communities on two common submerged macrophytes in Taihu Lake: diversity and host-specificity. Chinese Journal of Oceanology and Limnology, 2012, 30(2): 237-247.

[21] Hempel M, Grossart H P, Gross E M. Community composition of bacterial biofilms on two submerged macrophytes and an artificial substrate in a pre-alpine lake. Aquatic Microbial Ecology, 2009, 58(1): 79-94.

[22] Schramm A. In situ analysis of structure and activity of the nitrifying community in biofilms, aggregates, and sediments. Geomicrobiology Journal, 2003, 20(4): 313-333.

[23] Belyayeva P G. Role of phytoperiphyton in organic matter production and Nitrogen cycle in river ecosystems (review). Hydrobiological Journal, 2013, 49(5): 12-23.

[24] Zhao D Y, Luo J, Zeng J, Wang M, Yan W M, Huang R, Wu Q L L. Effects of submerged macrophytes on the abundance and community composition of ammonia-oxidizing prokaryotes in a eutrophic lake. Environmental Science and Pollution Research, 2014, 21(1): 389-398.

[25] Eriksson P G, Weisner S E B. An experimental study on effects of submersed macrophytes on nitrification and denitrification in ammonium-rich aquatic systems. Limnology and Oceanography, 1999, 44(8): 1993-1999.

[26] Trimmer M, Engström P, Thamdrup B. Stark contrast in denitrification and anammox across the deep Norwegian trench in the Skagerrak. Applied and Environmental Microbiology, 2013, 79(23): 7381-7389.

[27] Yin G Y, Hou L J, Zong H B, Ding P X, Liu M, Zhang S F, Cheng X L, Zhou J L. Denitrification and anaerobic ammonium oxidization across the sediment-water interface in the hypereutrophic ecosystem, Jinpu Bay, in the Northeastern Coast of China. Estuaries and Coasts, 2015, 38(1): 211-219.

[28] Tonkin J D, Death R G, Barquín J. Periphyton control on stream invertebrate diversity: is periphyton architecture more important than biomass?. Marine and Freshwater Research, 2014, 65(9): 818-829.

[29] Nishihara G N, Ackerman J D. The effect of hydrodynamics on the mass transfer of dissolved inorganic carbon to the freshwater macrophyte *Vallisneria americana*. Limnology and Oceanography, 2006, 51(6): 2734-2745.

[30] Rahalkar M, Deutzmann J, Schink B, Bussmann I. Abundance and activity of methanotrophic bacteria in littoral and profundal sediments of lake constance (Germany). Applied and Environmental Microbiology, 2009, 75(1): 119-126.

[31] Revsbech N P, Nielsen L P, Christensen P B, Sørensen J. Combined oxygen and nitrous oxide microsensor for denitrification studies. Applied and Environmental Microbiology, 1988, 54(9): 2245-2249.

[32] Schreiber F, Polerecky L, de Beer D. Nitric oxide microsensor for high spatial resolution measurements in biofilms and sediments. Analytical Chemistry, 2008, 80(4): 1152-1158.

[33] Wang Y C, Li Z K, Zhou L, Feng L L, Fan N W, Shen J. Effects of macrophyte-associated nitrogen cycling bacteria on denitrification in the sediments of the eutrophic Gonghu Bay, Taihu Lake. Hydrobiologia, 2013, 700(1): 329-341.

[34] 宋玉芝, 黄瑾, 秦伯强. 附着生物对太湖常见的两种沉水植物快速光曲线的影响. 湖泊科学, 2010, 22(6): 935-940.

[35] Jones J I, Eaton J W, Hardwick K. The influence of periphyton on boundary layer conditions: a pH microelectrode investigation. Aquatic Botany, 2000, 67(3): 191-206.

[36] Asaeda T, Sultana M, Manatunge J, Fujino T. The effect of epiphytic algae on the growth and production of *Potamogeton perfoliatus* L. in two light conditions. Environmental and Experimental Botany, 2004, 52(3): 225-238.

[37] Laugaste R, Lessok K. Planktonic algae and epiphyton of the littoral in lake Peipsi, estonia. limnologica-ecology and management of inland waters, 2004, 34(1/2): 90-97.

[38] Harwell M C, Havens K E. Experimental studies on the recovery potential of submerged aquatic vegetation after flooding and desiccation in a large subtropical lake. Aquatic Botany, 2003, 77(2): 135-151.

[39] Roberts E, Kroker J, Körner S, Nicklisch A. The role of periphyton during the re-colonization of a shallow lake with submerged macrophytes. Hydrobiologia, 2003, 506-509(1/3): 525-530.

[40] Liboriussen L, Jeppesen E. Temporal dynamics in epipelic, pelagic and epiphytic algal production in a clear and a turbid shallow lake. Freshwater Biology, 2003, 48(3): 418-531.

[41] 秦伯强, 高光, 朱广伟, 张运林, 宋玉芝, 汤祥明, 许海, 邓建明. 湖泊富营养化及其生态系统响应. 科学通报, 2013, 58(10): 855-864.

[42] Fritioff Å, Kautsky L, Greger M. Influence of temperature and salinity on heavy metal uptake by submersed plants. Environmental Pollution, 2005, 133(2): 265-274.

[43] Demırezen D, Aksoy A. Accumulation of heavy metals in *Typha angustifolia* (L.) and *Potamogeton pectinatus* (L.) living in Sultan Marsh (Kayseri, Turkey). Chemosphere, 2004, 56(7): 685-696.

[44] Pandey L K, Kumar D, Yadav A, Rai J, Gaur J P. Morphological abnormalities in periphytic diatoms as a tool for biomonitoring of heavy metal pollution in a river. Ecological Indicators, 2014, 36(1): 272-279.

[45] Marks J C, Lowe R L. Interactive effects of nutrient availability and light levels on the periphyton composition of a large oligotrophic lake. Canadian Journal of Fisheries and Aquatic Sciences, 1993, 50(6): 1270-1278.

[46] van Dijk G M. Dynamics and attenuation characteristics of periphyton upon artificial substratum under various light conditions and some additional observations on periphyton upon *Potamogeton pectinatus* L. Hydrobiologia, 1993, 252(2): 143-161.

[47] Özkan K, Jeppesen E, Johansson L S, Beklioglu M. The response of periphyton and submerged macrophytes to nitrogen and phosphorus loading in shallow warm lakes: a mesocosm experiment. Freshwater Biology, 2010, 55(2): 463-575.

[48] Berninger U G, Huettel M. Impact of flow on oxygen dynamics in photosynthetically active sediments. Aquatic Microbial Ecology, 1997, 12(3): 291-302.

[49] Hart D D, Biggs B J F, Nikora V I, Flinders C A. Flow effects on periphyton patches and their ecological consequences in a New Zealand river. Freshwater Biology, 2013, 58(8): 1588-1602.

[50] Binzer T, Borum J, Pedersen O. Flow velocity affects internal oxygen conditions in the seagrass *Cymodocea nodosa*. Aquatic Botany, 2005, 83(3): 239-247.

[51] Nishihara G N, Ackerman J D. Diffusive boundary layers do not limit the photosynthesis of the aquatic macrophyte *Vallisneria americana* at moderate flows and saturating light levels. Limnology and Oceanography, 2009, 54(6): 1874-1882.

[52] Allanson B R. The fine structure of the periphyton of *Chara sp.* and *Potamogeton natans* from Wytham Pond, Oxford, and its significance to the macrophyte-periphyton metabolic model of R. G. Wetzel and H. L. Allen. Freshwater Biology, 1973, 3(6): 535-542.

[53] Rogers K H, Breen C M. Effects of epiphyton on *Potamogeton crispus* L. leaves. Microbial Ecology, 1981, 7(4): 351-363.

[54] 刘凯辉, 张松贺, 吕小央, 郭川, 韩冰, 周为民. 南京花神湖3种沉水植物表面附着微生物群落特征. 湖泊科学, 2015, 27(1): 103-112.

[55] Larson C, Passy S I. Spectral fingerprinting of algal communities: a novel approach to biofilm analysis and biomonitoring. Journal of Phycology, 2005, 41(2): 439-546.

[56] Fang F, Yang L Y, Gan L, Guo L Y, Hu Z X, Yuan S J, Chen Q K, Jiang L J. DO, pH, and Eh microprofiles in cyanobacterial granules from Lake Taihu under different environmental conditions. Journal of Applied Phycology, 2014, 26(4): 1689-1699.

[57] Kühl M, Polerecky L. Functional and structural imaging of phototrophic microbial communities and symbioses. Aquatic Microbial Ecology, 2008, 53(1): 99-118.

[58] Nakamura Y, Satoh H, Okabe S, Watanabe Y. Photosynthesis in sediments determined at high spatial resolution by the use of microelectrodes. Water Research, 2004, 38(9): 2440-2448.

[59] Babauta J T, Atci E, Ha P T, Lindemann S R, Ewing T, Call D R, Fredrickson J K, Beyenal H. Localized electron transfer rates and microelectrode-based enrichment of microbial communities within a phototrophic microbial mat. Frontiers in Microbiology, 2014, 5(11): 11.

[60] Tan S Y, Yu T, Shi H C. Microsensor determination of multiple microbial processes in an oxygen-based membrane aerated biofilm. Water Science and Technology, 2014, 69(5): 909-914.

[61] 王文林, 王国祥, 万寅婧, 夏劲, 唐晓燕, 陈昕, 梁斌, 庄巍. 光照和生长阶段对菖蒲根系泌氧的影响. 生态学报, 2013, 33(12): 3688-3696.

[62] Tu Q C, Yu H, He Z L, Deng Y, Wu L Y, Van Nostrand J D, Zhou A F, Voordeckers J, Lee Y J, Qin Y J, Hemme C L, Shi Z, Xue K, Yuan T, Wang A J, Zhou J Z. GeoChip 4: a functional gene-array-based high-throughput environmental technology for microbial community analysis. Molecular Ecology Resources, 2014, 14(5): 914-928.